Oviposition, Fecundity, and Larval Development of Three Sacoglossan Opisthobranchs from the Northumberland Coast, England

BY

FU-SHIANG CHIA [1]

Dove Marine Laboratory and Department of Zoology, University of Newcastle upon Tyne, England

(4 Plates)

INTRODUCTION

Along the Northumberland coast, three species of sacoglossan opisthobranchs, *Limapontia capitata* (Müller, 1773), *L. depressa* (Alder & Hancock, 1862) and *Acteonia cocksi* Alder & Hancock, 1848, are to be found. Although their distribution is restricted (Gascoigne, 1952, 1956), a large number of specimens can be secured from localities not far from the Dove Marine Laboratory.

A number of papers have been published on various aspects of the reproductive biology of these species. Notable are those of Pelseneer (1899) and Colgan (1911, 1912) on the development of *Acteonia cocksi*; Thorson (1946) on the larval morphology of *Limapontia capitata*; Gascoigne (1956) on the reproductive system and mating behaviour of *L. capitata* and *A. cocksi,* and Miller (1962) on the reproductive cycle of *A. cocksi* and *L. capitata*. More recently, Seelemann (1967) described the larval development and metamorphosis of *L. depressa*. Scattered information on opisthobranch development has been summarized and tabulated by Thompson (1967). Despite these studies, knowledge of developmental chronology and fecundity of these species is still lacking or fragmentary at best. The present paper describes laboratory observations on their oviposition, fecundity, and larval development.

ACKNOWLEDGMENT

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COLLECTION

Limapontia capitata and *Acteonia cocksi* were collected from shallow rocky pools at the north side of the Cullercoats Bay or from those at St. Mary's Island. In these pools, there is plenty of green algae, *Cladophora* or *Cladophora* and *Enteromorpha,* upon which the animals feed. Since both opisthobranch species are similar in size and color, it is difficult to distinguish them in the field without the aid of magnifying glasses. However, behaviorally, *A. cocksi* are usually seen crawling on the substratum whereas *L. capitata* are found on the algae.

In the laboratory the animals were kept in small finger bowls and provided with a few branches of *Cladophora,* at a temperature of 10 - 14° C. However, they can survive equally well at room temperature (19 - 21° C) and in one half of the salinity of normal sea water.

Limapontia depressa was collected from the salt marshes at Alnmouth where it is flooded only during spring tides. They usually aggregate into small clusters on the bed of *Vaucheria,* which is their major food. The color of this animal varies from lemon yellow to green and black, matching well with that of their environment. In the laboratory they were kept in finger bowls with a layer of *Vaucheria* on coarse sand. More information on the collection is summarized in Table 1.

[1] Present address: Department of Zoology, University of Alberta, Edmonton, Alberta, Canada

Table 1

DATA OF COLLECTION

Date	Locality	Species	Number of Animals Collected	Average Length (in mm) of the Animals
April 1969				
2	Cullercoats	*Limapontia capitata*	17	3.1
2	St. Mary's	*Acteonia cocksi*	2	3.9
		Limapontia capitata	25	3.4
8	St. Mary's	*Acteonia cocksi*	14	4.2
11	Alnmouth	*Limapontia depressa*	110	4.5
16	St. Mary's	*Limapontia capitata*	79	4.3
		Acteonia cocksi	51	4.7
May 1969				
15	Alnmouth	*Limapontia depressa*	170	?
22	Cullercoats	*Limapontia capitata*	numerous	1.2

OVIPOSITION AND FECUNDITY

The three sacoglossans are hermaphroditic and fertilization is by hypodermic impregnation (GASCOIGNE, 1956). One copulation is apparently sufficient to fertilize the eggs of several spawn masses within the breeding season.

Limapontia capitata:

Two days after capture, the animal began to lay eggs. The eggs are enclosed in a sausage-like jelly mass which is attached either on the algae or on the glassware. The size of the spawn mass varies depending on the number of eggs it contains. A large spawn mass with 500 eggs is about 0.7 mm in diameter and 2 mm long, while a small spawn mass with less than 50 eggs is spherical and ½ mm in diameter. The jelly material is homogeneously transparent, adhesive on the surface and usually covered with debris in the natural habitat. In large spawn masses the eggs are spirally arranged into regular rows but this is not so in small spawn masses. The eggs do not attach to each other nor the jelly mass envelope; they are suspended free in a fluid in the lumen of the jelly. Upon damage to the jelly, the eggs usually flow out freely. An individual egg is enclosed in a capsule which is about 100μ in diameter, whereas the egg itself is only 82μ in diameter. The fluid inside the capsule is either transparent or with suspended granular material (albumen). This material, however, does not serve any essential function as the eggs without albumen develop equally well. The egg is yellowish in color and is perfectly spherical, although the capsule in most cases is oval in shape. Most of the capsules contain only one egg, but up to 4 eggs in one capsule have been observed occasionally.

In order to study the fecundity, 20 animals collected on April 2nd from St. Mary's Island were placed in one finger bowl with 150 ml sea water and some *Cladophora*. The culture dish was maintained at the temperature of 10 to 13° C and was examined daily. Spawn masses were removed, and the number of spawn masses and the number of eggs of each spawn mass was counted and recorded. After one month in captivity, the animals were getting smaller and fed less actively and most of them died in the second month.

Table 2

RECORD OF EGG-LAYING BY 20 ANIMALS OF *Limapontia capitata* WITHIN A MONTH

Date	Number of Egg Masses	Number of Eggs per Spawn Mass		Total Number of Eggs
		Range	Mean	
April				
4	2	244-720	482	964
5	7	250-700	382	2674
6	0			
7	8	180-600	362	2896
8	6	140-705	393	2358
9	0			
10	10	38-300	177	1770
11	5	105-180	124	620
12	3	108-163	134	402
13	10	65-170	114	1140
14	3	58-184	132	396
15	6	57-166	106	636
16	7	31-142	108	756
17	3	56-125	95	285
18	6	66-134	91	546
19	4	53-131	86	344
20	3	61-113	95	285
21	3	75- 85	81	243
22	7	45-114	76	532
23	1	63	63	63
24	1	71	71	71
25	0			
26	9	41- 93	67	603
27	0			
28	8	34- 68	44	352
May				
3	6	49- 65	55	330
Total	118			18 266

Table 2 shows that among the 118 spawn masses, the highest number of eggs per spawn mass is 720 and the lowest is 31. In general, the larger spawn masses were laid during the first 5 days after capture, and getting smaller and smaller thereafter. It further shows that each animal spawned on an average of 6 times during one month and that the average number of eggs laid by each animal is about 913.

Acteonia cocksi:

The spawn mass of *Acteonia cocksi* is essentially similar to that of *Limapontia capitata*. The eggs are, however, much larger than those of *L. capitata* and consequently there are only a few eggs in each mass. The egg capsule is oval in shape and measures 350μ ×550μ. The egg itself is spherical, yellow to orange in color and measures 200μ in diameter. There is always a granular and milky coloured albuminous material inside the capsule. It is likely that this is a dehydrated material which will be hydrated later to expand the egg capsule to give more room for locomotion to the developing embryo. This conclusion is supported by the observation that all albumen granules become liquefied at gastrula stage and in the meantime the egg capsule enlarges about 40% of its original size.

Among all the spawn masses I have examined, there was always one egg per capsule. The egg laying records of 14 animals collected on April 8 are given in Table 3, which shows that these animals laid 31 spawn masses or 323 eggs within a month. In other words, each animal laid only an average of 2 spawn masses or 23 eggs. As in *Limapontia capitata,* the animals were getting smaller and smaller after one month in captivity, and all died in the second month.

Table 3

RECORD OF EGG-LAYING BY 14 ANIMALS OF *Acteonia cocksi* WITHIN A MONTH

Date	Number of Egg Masses	Number of Eggs per Spawn Mass		Total Number of Eggs
		Range	Mean	
April				
12	1			19
14	3	10-20	15	46
15	3	17-26	21	63
16	4	7-23	17	68
17	1			10
22	1			2
23	5	6-17	9	45
26	2	5- 6	5	11
28	2	5-10	8	15
May				
3	3	4- 7	6	17
10	4	3- 6	4	17
12	2	4- 6	5	10
Total	31			323

Limapontia depressa:

The spawn mass of *Limapontia depressa* differs from that of *L. capitata* and *Acteonia cocksi* in several ways. First, the jelly mass appears to be lamellated, thinner, and more elastic. Secondly, the jelly mass tapered at one end (the end last out from the oviduct) into a fine point which bends into a hook. In most cases, the spawn mass lies parallel to the animal and since both are about the same colour, one often mistakenly interprets this as a mating pair. In the culture dish 2 or 3 spawn masses are often seen close by one animal, suggesting that one animal may lay more than one spawn mass within 24 hours. As in the other 2 species already described, there is again no clear preference as to where the egg mass is deposited; egg masses are found both above and underneath the algal layer as well as on the glassware or on the sand grains.

A large spawn mass, 2×5 mm in size, contains about 950 eggs and a small spawn mass of 0.5×1 mm in size contains only 73 eggs. The egg capsule, 120μ in diameter, contains in most cases only one egg, 80μ in diameter, but occasionally up to 4 eggs per capsule were found. Many egg capsules also contain granular albumen but this has apparently little nutritional value, as those eggs without albumen develop equally well.

Seventy animals collected on April 11, 1969 were placed in a small finger bowl on a layer of *Vaucheria*. The finger bowl was kept in high humidity but the animals were not immersed in water. The egg laying record of these animals within one month is summarized in Table 4. This table shows that the animals began to lay eggs 5 days after capture and within one month a total of 346 egg masses were deposited. Although I did not count the eggs in every spawn mass, it was estimated that the average number of eggs per spawn mass was about 450. This means that on the average each animal laid 5 spawn masses or 2250 eggs. This is more than double the number of eggs produced by each *Limapontia capitata.*

Table 4

RECORD OF EGG-LAYING BY 70 ANIMALS OF *Limapontia depressa* WITHIN A MONTH

Date:	April						May					
	11	16	18	20	22	24	26	28	3	5	10	12
Number of Spawn Masses laid	0	2	9	34	59	70	50	34	35	20	23	0

EFFECT OF LIGHT ON OVIPOSITION

During my observations on the oviposition of *Limapontia capitata* and *Acteonia cocksi,* the culture dishes were examined twice a day, once at about 10 o'clock in the morning and once at about 5 o'clock in the afternoon. All the spawn masses, with a few exceptions, were collected in the morning. Since the detailed chronology of the early development is known, the precise time of egg laying can be estimated from the stages of development. In this way it is discovered that most of the spawn masses were laid in the morning between about 6 and 9 o'clock. This led me to suspect that the change of illumination, switching from dark to light, might be responsible for inducing the spawning, which is the case for many invertebrates (see KUME & DAN, 1968). To test this observation, animals of both species, collected on April 16, 1969, were studied experimentally by subjecting 15 animals of each species to 3 conditions: constant light, constant dark, and normal day light cycles as control. The light and dark experimental groups were again exposed to normal day light cycles after 3 days. The result shows that continuous light or dark tends to repress the spawning, but the spawning frequency did not increase after returning to normal conditions. Hence, the egg laying behaviour in these species may be associated with the change of illumination, but artificial induction of spawning by control of light was not successful.

LARVAL DEVELOPMENT

As noted earlier, the larval morphology of these species is already known. This section presents information only on the chronology of development which has not been established in detail previously.

The morphology of developmental stages of *Limapontia capitata* and *L. depressa* is almost identical under laboratory conditions. The major events of development are summarized in Table 5 and illustrated in the accompanying 2 Plates. It is noted that it takes 12 days for *L. capitata* and 10 days for *L. depressa* to reach the hatching larval stage at the temperature of 10 - 14° C. At room temperature (19 - 21° C) the time was shortened to 8 days for *L. capitata* and to 7 days for *L. depressa.*

In contrast to that of *Limapontia,* the development of *Acteonia cocksi* is direct and a planktotrophic larva is lacking; the major developmental events are summarized in Table 6 and illustrated in 2 additional Plates accompanying this paper.

It is interesting to record that after hatching, the juveniles of *Acteonia cocksi* do not crawl away from the jelly mass; instead, they remain inside and feed actively on the egg capsules as well as on the inner layer of jelly mass. Two to 3 days pass before they begin to feed on the algae. At no stage of development is a larval shell observed.

Plate Explanation

Development of *Limapontia capitata*

Figure *1*: One and 2-cell stages showing polar bodies (pl. b.)
Figure *2*: 4-cell stage
Figure *3*: 4-cell stage, showing the presence of albumen (a)
Figure *4*: 16-cell stage, showing micromeres (mi) and macromeres (ma)
Figure *5*: Gastrula with polar bodies (pl. b.) and open blastopore (bl. p.)
Figure *6*: Veliger larvae before hatching

Plate Explanation

Development of *Limapontia depressa*

Figure *7*: One-cell stage showing polar bodies (pl. b.)
Figure *8*: One- and 2-cell stages
Figure *9*: 4-cell stage
Figure *10*: 8-cell stage, showing micromeres (mi) and macromeres (ma)
Figure *11*: Blastula, flattened along A - V axis
Figure *12*: Gastrula with open blastopore (bl. p.)
Figure *13*: Young veligers
Figure *14*: Veliger just before hatching

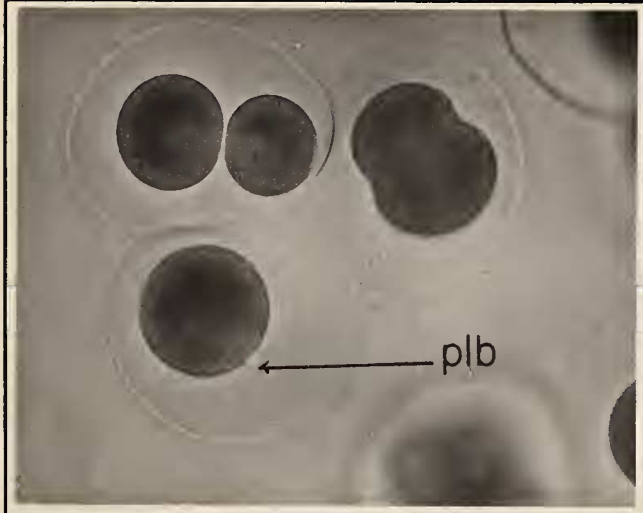


Figure 1

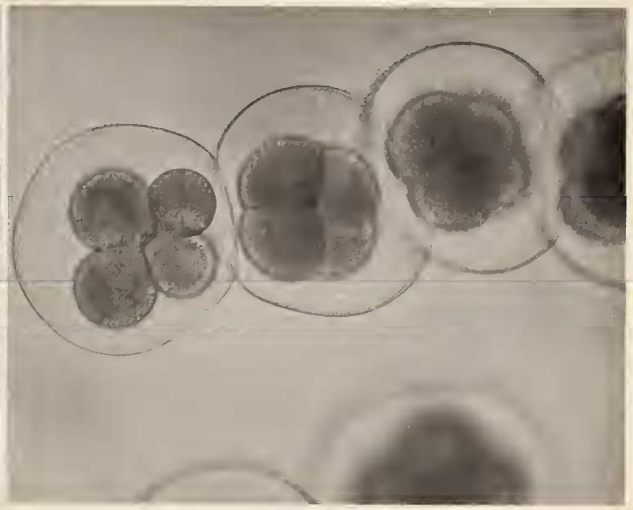


Figure 2

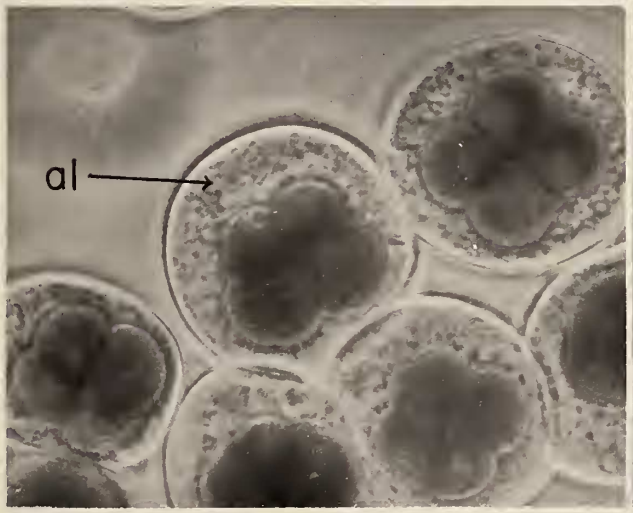


Figure 3

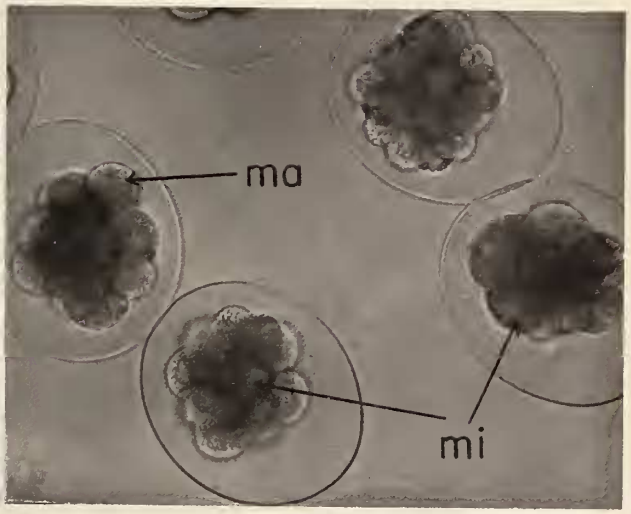


Figure 4

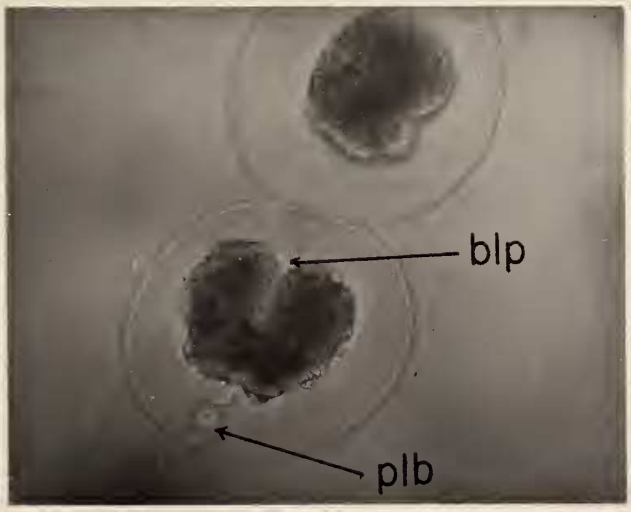


Figure 5

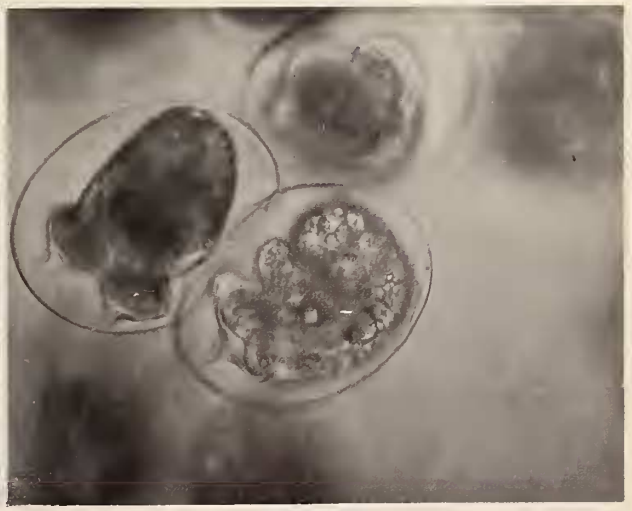
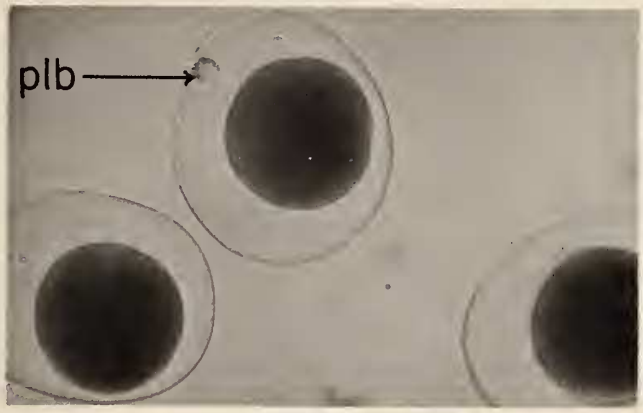


Figure 6



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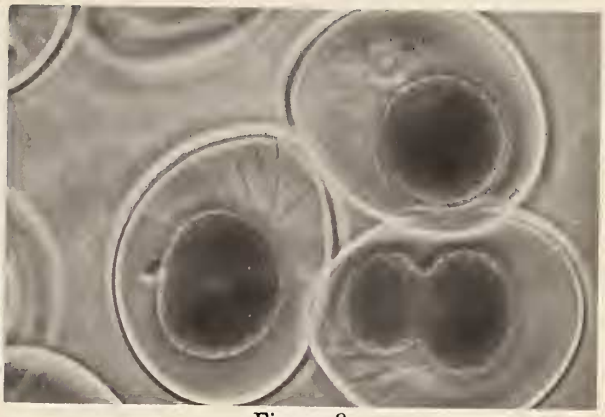
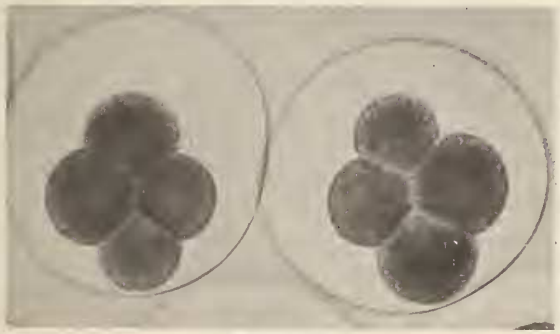


Figure 8



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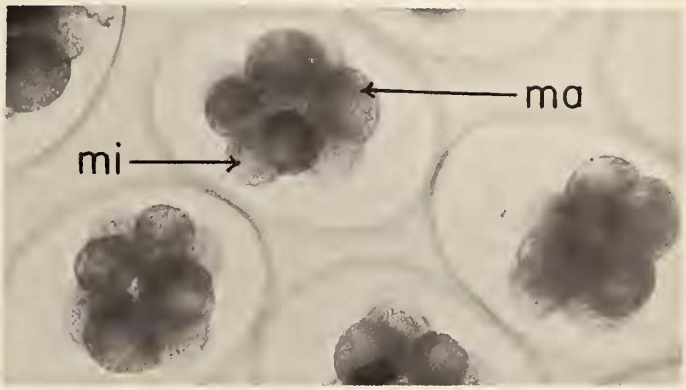


Figure 10

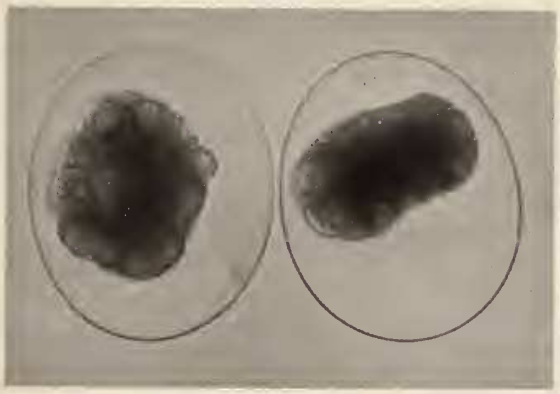


Figure 11

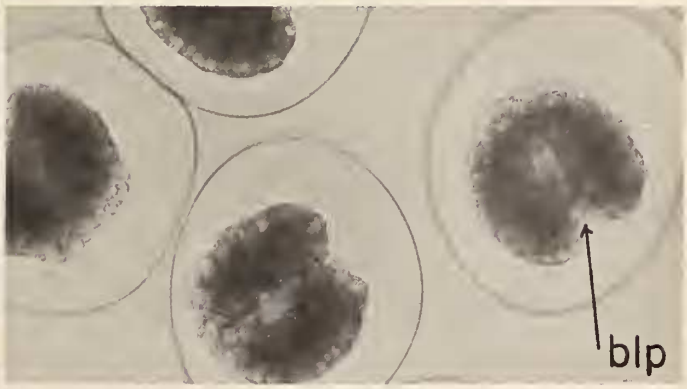
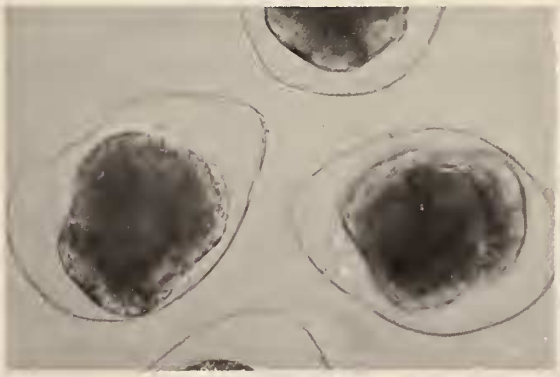


Figure 12



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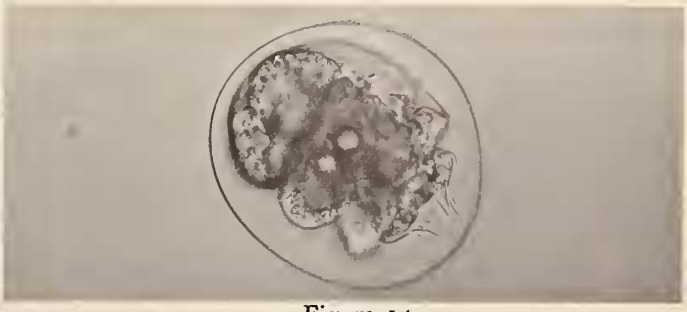

Figure 14